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Diurnal Vertical Migrations of Cod and Haddock

Candidate of Biological Sciences

K.G. Konstantinov

INTRODUCTION

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Diurnal vertical migrations are an important feature of the behaviour of cod and haddock, noticeably affecting the successes achieved in trawl fishing. It is characteristic of these fishes to ascend to the middle strata with the onset of darkness and to descend to the bottom during the daylight hours. As a rule, therefore, trawl catches are heavier by day and smaller at night.

Diurnal vertical migrations of cod and haddock have not been adequately studied. Published reports on fish migrations [70,100] discuss only the horizontal migrations. They do not even touch upon vertical migrations. In the very complete and detailed studies of the biology and fishing of cod fish, diurnal vertical migrations are the subject of only a few lines in all [46,49,80]. Yet, as E.V. Borutskii [12,13] has correctly pointed out, vertical migrations of plankton have been studied to a much

*The figures in the right-hand margin are page numbers in the original (Tr.).

greater degree than have horizontal.

The question arises: why have vertical migrations of fishes, which are extremely important commercially, been studied to a much lesser extent than vertical migrations of plankton? The answer lies mainly in the following. When investigating vertical migrations of plankton, no serious methodological difficulties are encountered. It is easy to make a qualitative and quantitative count of the plankton at the depths in which we are interested. Whereas the procedures for studying vertical migrations of plankton have been described in a number of manuals [73], until now there has been no dependable gear for taking a fish in the mid-water (fixed nets, long-lines and hand lines catch fish of by no means all species and sizes).

During the last two decades, hydroacoustic methods have been used for ichthyological studies with ever increasing success. With their help it has proved possible in many instances to follow in detail the diurnal vertical migrations of commercial fishes. It is, of course, true that the behaviour of fishes cannot be studied solely on the basis of single readings of hydroacoustic instruments. What are needed are in-depth studies of the biology of the fish and of the mechanisms governing its migration [58].

Actually, vertical migrations (as also all other migrations and all fish behaviour in the broad sense) are governed by environmental conditions and the state of the fish itself. In order to explain, predict and utilise diurnal vertical migrations it is necessary to identify the role of hydrological, hydrochemical and meteorological factors, and to take into consideration the amount of food in the digestive tract, the

overall condition and sexual maturity of the fish, and also the composition and distribution of its food sources. Meanwhile, it is impossible to obtain information on the internal state of the fish and the conditions of the environment through the use of hydroacoustic instruments, even though they sometimes yield an extremely precise fix on the position and movement of aggregated (or even an individual) fish. It follows from 63
this that investigations conducted solely by means of a single hydroacoustic technique are purely descriptive and registrative in character and do not reveal the causes of the phenomenon being observed.

For studying the diurnal vertical migrations of fishes, we need an interdisciplinary approach. Only the integrated efforts of hydrologists and hydrochemists, planktonologists and benthologists, sonar specialists and ichthyologists can provide an exhaustive description of the migrations of a fish in the mid-water, and reveal the patterns and causes of these.

In 1953 and 1954 an interdisciplinary study of the diurnal vertical migrations of cod and haddock was conducted by co-workers of the N.M. Knipovich Polar Scientific Research Institute of Sea Fisheries and Oceanography (PINRO), under the direction of N.A. Maslov. The main results of the study, augmented by certain findings from other years, are discussed in the present article.

THE EFFECT OF DIURNAL VERTICAL MIGRATIONS OF COD AND HADDOCK ON TRAWL CATCHES

In the ichthyological literature, references to the presence of cod and haddock in the middle layers and even the surface layers of the water are fairly numerous. Jensen and Hansen [93] mention that the Greenland cod frequently pursues capelin just below the surface. This is also

reported with respect to the Barents Sea haddock by V.I. Zatsepin [23] and the Barents Sea cod by N.S. Petrov and V.I. Zatsepin [24]. The authors cite instances of capelin trap nets being plundered by cod off the coast of the Murman Coast. Experimental fishing by fixed gill nets and long-lines at various depths also attests to the presence of cod in the mid-water [31,46,48]. In the Gulf of Maine, it sometimes proved possible to take a large cod with a gaff, at the very surface [76]. Rassmussen [105] reports that in 1953, on the West Greenland Banks commercial concentrations of cod stayed predominantly in the middle layers of water and were fished by Norwegian fishermen using long-lines. Finally, cases are known of cod getting into drifter nets at depths greater than 1,000 m (Norwegian Sea).

Convincing evidence of the ascent of cod and haddock into the mid-water is afforded by periodic fluctuations of trawl catches. If a trawler is seining a stable concentration of a fish over a protracted period, with the daytime catches proving invariably larger than the nighttime, we are correct in surmising regular ascents of the fish to horizons that are not accessible to fishing by bottom-trawl. This hypothesis becomes all the more probable when the catches of an entire group of trawlers exhibit almost uniform and simultaneous variations over a vast expanse of water. In this case, the fluctuations in the catches can definitely not be attributed to the fish having migrated from one region to another.

Buckmann [77], in describing the voyage of a fishing trawler in the Barents Sea, interpreted the fluctuations in the catches as being precisely due to nocturnal ascents of haddock into the mid-water. A similar explanation was given by Lucas [96] for the excess of daytime

over nighttime catches when fishing for herring with a trawl. Driscoll [84] is another author who considers diurnal fluctuations in trawl catches to be a consequence of migrations of cod and haddock into mid-water. References to diurnal vertical migrations of fishes are also found in some of the fishing instruction manuals. For example, the provisional regulations with respect to fishing trawlers, published by Murmanrybprom* in 1947, make mention of vertical migrations which lower nighttime catches.

Thus, the fact that there are diurnal fluctuations in trawl catches has become common knowledge. Until now, however, this phenomenon has not been precisely quantified.

In an attempt to arrive at a quantitative estimate of the effect of vertical migrations on trawl catches, we made a search of original fishing documents. The navigating officers of the Murmansk trawler fleet enter the results of each trawl in standard returns on fishing voyages 64
(Form No. 2). On the basis of such entries it is easy to reconstruct when and where the trawling was done, for how long it continued and what the catch was. The navigator on duty visually determines the size of the catch (recalculated for semi-finished products). On completion of the voyage a correction is made to these operating data, since the weight of an unloaded fish is usually not fully in agreement with the preliminary estimate made for the fishing industry.

An analysis of the fishing voyage returns makes it possible to trace the variation in the catches throughout the day. We spread all of the trawlings considered over the following four-hour intervals:

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*A Soviet acronym for the Murmansk Fishing Industry (Tr.).

0001-0400 hours, 0400-0800 hours, 0800-1200 hours, 1600-2000 hours and 2000-2400 hours. Trawls embracing two contiguous intervals we assigned to the interval which accounted for the more prolonged portion of trawling. For each interval, the average catch (in semi-finished products) in an hour of trawling was calculated. We did not make corrections to the thus derived indices, since what was of interest to us was not so much the absolute size of the catch as its variation over the 24-hour period. In all, about 13,000 trawlings performed by Murmansk fishing trawlers in 1953 were taken into account.

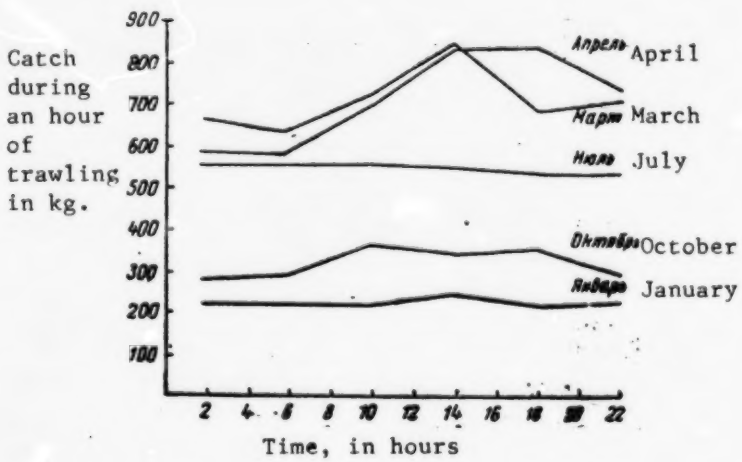

Fig. 1. Trawl catches on the Murmansk Bank at various times of the day

Illustrated in fig. 1 are the diurnal dynamics of catches on the Murmansk Bank (summated for all of its slopes). It will be seen that in January the hourly trawling catches are practically identical at any time of the day (night). In March and April the catches reach a peak during the daytime. In July the catches again become identical in all of the

four-hour intervals: the average catch in an hour of trawling ranges within exceedingly narrow limits - between 216 kg (0800-1200 hours) and 250 kg (1200-1600 hours). In October, a difference exists between the daytime and the nighttime catches, even though it is not particularly significant. In the other months of 1953, the fleet was either largely inactive on the Murmansk Bank or did not fish at all.

Thus, the trawling catches in the winter and summer months were fairly constant throughout the 24-hour period, and in spring and fall the daytime catches were greater than the nighttime. The difference can be very pronounced. For example, in April of 1953 the daytime catch exceeded the nighttime by more than 40%.

Presented in table 1 are the catches (semi-finished products) obtained at various time of the day (night) on the Gusinaya and Medvezh'e Banks. In August and November the daytime catches proved to be somewhat higher than those made at night, but the difference was very small. In these months the illumination of the sea is almost constant throughout the 24-hour period (in August the nights are still short, and in November there is almost no daylight). In January and December there were almost no diurnal fluctuations in the catches, which is readily understandable, 65 since the Polar Night predominates in the Barents Sea during these months.

Diurnal fluctuations in the catches are revealed not only when correlating the results of many trawlings, but also when analysing the work of a single trawler. During the 57th voyage of the PINRO Expeditionary Ship "Persei-2", several series of trawls were conducted at a fixed fishing site, along with a detailed ichthyological analysis of the catch. The results of one of these series are adduced in table 2.

Table 1

Catches in kg during an hour of trawling at various times of the day

Hours	Gusinaya Bank		Medvezh'e Bank	
	August	November	January	December
0—4	494	156	358	617
4—8	602	174	396	682
8—12	654	269	396	615
12—16	621	239	356	684
16—20	641	205	328	700
20—24	606	209	364	700

Table 2

Itemised catches by bottom trawl on the southwest slope of the Murmansk Bank in 1953

Date	Return time of stopper in hrs & mins.	Caught		
		Cod	Haddock	Both
5 April	17—05	1029	1326	2355
5	20—10	488	276	764
6	1—20	34	88	122
6	10—55	53	356	409
6	12—35	100	703	803

All of the trawlings lasted for an hour and were performed at a buoy at the same depth (the 35 soundings executed during the trawlings indicated a minimum depth of 155 m and a maximum depth of 170 m). The weather remained murky throughout the entire period and the sky was continually overcast.

The derived data attest to the dependence of the size of the catch on the alternation of day and night. At the 70th parallel, where the work was carried out, the difference between the daytime and nighttime illumination of the sea was clearly defined at the beginning of April. The difference between the daytime and nighttime catches proved to be just as pronounced.

Similar results were also derived in another series of trawls, performed during the same voyage. These trawlings also lasted for an hour and were performed at a buoy, at practically the same depths (the least of the measured depths was 136 m, the greatest - 162 m). Cloudiness during the daytime trawlings was estimated to be from 5 to 7 on a 10-point scale. The number of fishes caught and the weight of the catch (the latter according to a visual estimate by the duty navigator) showed a tendency to increase during the day and to fall at night (table 3).

Table 3

Catches (itemised) by bottom trawl in the western coastal region in 1953

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Date	Return time of stopper	Caught			Weight of catch in cwt* (semi-finished products)
		Cod	Haddock	Both	
15 April	3–05	595	38	633	2
15 "	7–00	1208	462	1670	4
15 "	10–45	2079	474	2553	7
15 "	19–05	547	289	836	2
15 "	21–40	1196	432	1628	3
15 "	23–25	544	470	1014	2
16 "	2–00	1012	394	1436	2

That it is precisely the illumination of the sea, rather than any accompanying factor, which influences the catches is demonstrated by the

*Revisor's note. "Cwt" here refers to the Soviet centner, which is 100 kg.

results of the 58th voyage of the "Persei-2". The voyage lasted from May 1 to 12 inclusive. At that time of the year the difference in the illumination of the sea during the day and at night is barely noticeable. Accordingly, the series of trawlings on Kil'da Bank revealed only very slight differences in the sizes of the daytime and nighttime catches. On the other banks, fishing progress was equally successful by day and at night.

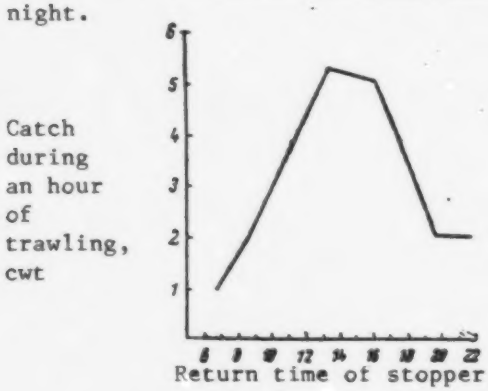

Fig. 2. Catches during an hour of trawling in Motovskii Gulf on May 3, 1953

However, trawlings performed on May 3 off the north shore of Motovskii Gulf distinctly indicated an excess of the daytime over the nighttime catches (fig. 2) in the presence of fully stable meteorological conditions, namely, a calm sea and continuous cloudiness. Thus, at the beginning of May the diurnal periodicity of the catches, which did not show up as being greater in the open sea, was still being maintained in Motovskii Gulf on account of its steep shores having generated a certain amount of shade. In the daytime, when the sun was high, the shores did not affect the illumination of the sea. At night, however, a considerable amount of shade was cast onto the surface of the Gulf. Thus was preserved a diurnal periodicity of the illumination which resulted in regular migrations of the fish into the mid-water, which in turn, had a detrimental effect on the sizes of the trawl catches.

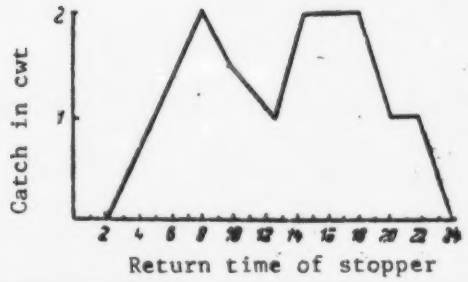

Fig. 3. Trawl catches on Kanin Bank, October 23, 1954

Shown in fig. 3 are the catch dynamics at the diurnal observation station off Kanin Nos. The trawlings were performed on October 23, 1954 at depths of 53-64 m. That the trawling site remained constant was ensured by visual bearings on Kanin lighthouse. The catches consisted of haddock of a uniform size distribution: about 40% of the specimens were 35-40 cm in length, with 85% of them belonging to the 1950 year-class.

As will be seen from the sketch, the series of trawlings revealed 67
a diurnal fluctuation in the catches. Consequently, these findings also illustrate the relationship between changes in the illumination and the size of the trawl catches.

HYDROACOUSTIC OBSERVATIONS OF DIURNAL VERTICAL MIGRATIONS

As was indicated earlier, regular fluctuations in trawl catches must be regarded as a consequence of the periodic migration of cod and haddock from the near-/bottom layers into the middle layers of the water. Such an interpretation is convincingly strengthened by hydroacoustic observations.

The use of hydroacoustics for the /scouting and study of fish is a comparatively recent development. The history and current status of hydroacoustics as applied to the fishing industry has been the subject of a quite detailed description by Hodgson and Fridriksson [92], who unfortunately, did not include in their book any information on the work

done by Soviet scientists in this field. Today, recording echo sounders have become firmly entrenched in the practice of spotting fish concentrations and doing ichthyological research. In the overwhelming majority of instances, however, the targets of a hydroacoustic survey and study are restricted to pelagic fishes, primarily herring. It is precisely in herring fishing that the greatest successes have been achieved through the use of recording echo sounders [5, 20, 71, 72, 74, 75, 78, 86, 91, 104, 106, 114]. Echo sounders have also been fruitfully used in the spotting and fishing of kilka, sprats and sardines [3, 69, 86, 91].

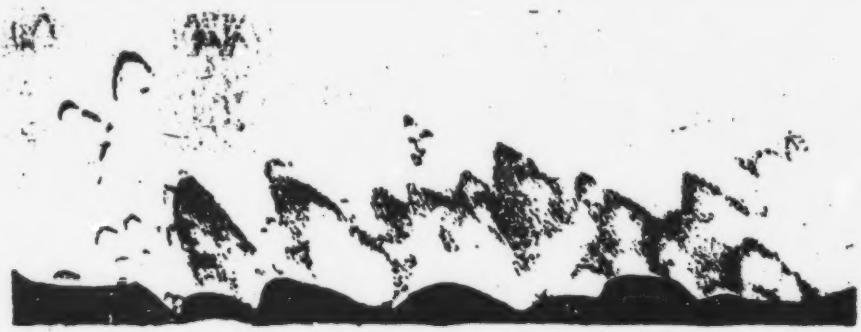

Fig. 4. Distribution of cod in the mid-water at 1320 hours on October 12, 1954 (sketched from an echogram)

In recent years there has been a considerable accumulation of data on hydroacoustic observations of cod and haddock. Concentrations of these fishes are recorded by echo sounders both on the bottom and in the mid-water. It will be recalled that the first time the echo sounder was used successfully was for the recording of cod that had ascended into the middle horizons [111]. The use of recording echo sounders greatly facilitates the spotting, fishing and study of cod and haddock [64]. Without digressing here into a discussion of the vast body of material derived from echo sounding, we would note only that, in many instances

it proves possible to follow in detail all phases of the diurnal vertical migration of cod and haddock.

Illustrated in the accompanying echograms (figs. 4 and 5) is the distribution of cod in the mid-water above one and the same area of the bottom during the day and in the evening. The echograms demonstrate quite graphically the ascent of the cod into the middle horizons with the onset of darkness. It stands to reason that such a migration of fish has a drastic effect on the sizes of the trawling catches.

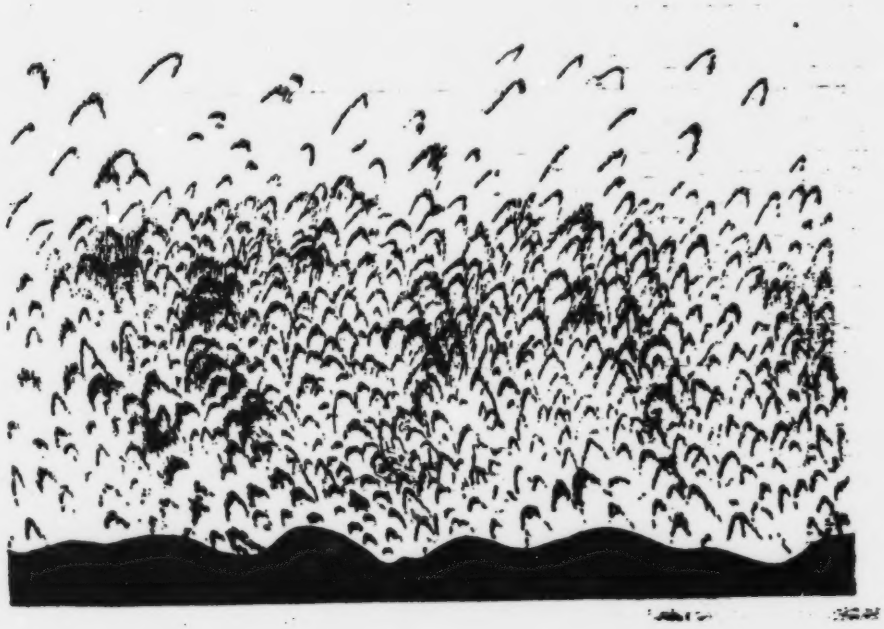

Fig. 5. Distribution of cod in the mid-water at 1830 hours on October 12, 1954 (sketched from an echogram)

THE EFFECT OF HYDROMETEOROLOGICAL FACTORS ON DIURNAL VERTICAL MIGRATIONS OF AQUATIC ANIMALS

The findings discussed in the preceding sections convincingly attest to the critical effect of fluctuations in lighting intensity on the diurnal vertical migrations of fishes. Also evident is the role played by light in the regulation of diurnal vertical migrations of the zooplankton. Hickling [90], having studied the biology of the Atlantic euphausiids, considers that light is a fundamentally important factor in controlling diurnal vertical migration. A similar view is expressed by Russell [107-109], who cites as examples planktonic crustacea and immature herring. V.N. Nikitin [51,53] reached the conclusion that light plays an important role in vertical migrations of the Black Sea zooplankton, forcing the migrants to surmount very steep temperature gradients.

V.G. Bogorov [7, 9-11], made a comparison of the vertical distributions of the plankton of the polar seas in the various seasons. He points out that diurnal migrations are only accomplished when there is alternating light and darkness, for example, in summer in the White Sea and in the autumn in the Barents Sea and the seas of the high latitudes in general. References to such migrations have also been reported for the Shokal'skii Straits and the Vil'kitskii Straits by V.L. Khmyznikova [66].

That diurnal vertical migrations of the zooplankton are primarily due to stimulations by light is also regarded as proven by S.N. Skadovskii [62,63]. By surgically removing the statocysts from mysids, Foxon [85] observed that the vertical migrations of the animals that formed the subject of the experiment persisted under the influence of light.

In recent years hydroacoustic techniques have made it possible to record regular vertical migrations of the zooplankton under the influence of diurnal fluctuations in the illumination [17,79,83,99,112].

In the course of assembling the material for the present article, vertical migrations of zooplankton were also studied. Used for this purpose was a net of closely woven gauze which was fastened to the upper head line of the trawl, and consequently seined the demersal layers of the water.

Presented in table 4 are the results of a series of trawls performed during the 57th voyage of "Persei-2" at a fixed location (collection and processing of the materials by S.S. Drobysheva). 69

Table 4

Numbers of euphausiids in the near-bottom layer (during 1 hour of fishing with the trawl net)

Date	Return time of stopper	Number of euphausiids	Date	Return time of stopper	Number of euphausiids
15 April	19–05	214	16 April	3–50	54
15 "	21–40	211	16 "	7–25	366
15 "	23–25	0	16 "	10–40	1494
16 "	2–00	1	16 "	14–15	242

It will be seen from table 4 that the number of euphausiids near the bottom changed regularly in the course of the 24-hour period, increasing during the day and decreasing at night. There can be no question that what was being manifested here was an ascent by the euphausiids into the mid-water with the onset of darkness and their descent to the bottom at daybreak.

Thus, the role of light in the regulation of diurnal vertical migrations of fishes and the zooplankton has been made absolutely clear by a number of investigations.

In order to elucidate the question of the effect of other hydrometeorological factors, foremost among which are the temperature and chemism of the water, a series of water samples were taken from various horizons at a fixed position with simultaneous measurement of the temperature. The samples obtained were subjected to an immediate and quite extensive chemical analysis. This made it possible to compare the diurnal vertical migrations of the fish with fluctuations in the temperature and chemism of the water in the various layers.

Presented in table 5 are data of the kind that were obtained during the 57th voyage of the "Persei-2" at one of the diurnal stations. Judging from the trawl catches and recordings of the echo sounder in the area of the study, the cod and haddock had completed typical diurnal vertical migrations. Is it possible that these migrations were related in some way to the temperature and chemical composition of the different layers of water?

The data in table 5 force us to respond to this question in the negative. As a matter of fact, none of the indices has a diurnal rhythm, coinciding albeit approximately with the diurnal rhythm of the vertical migrations of a fish. Many of the properties of the water that were studied were found to be constant. Their deviation from the mean diurnal level was no more than a fraction of a percent. The other indices, for example the temperature near the bottom, fluctuated more markedly, but these fluctuations are not fully correlated with the periodicity of the vertical migrations.

During the next voyage of the "Persei-2", although the thermal and chemical conditions were in general unchanged, the diurnal vertical migrations of the fish and the zooplankton had ceased.

Another series of hydrological and hydrochemical analyses was made on October 30, 1954 in the north-central region. To ensure that the ship remained on station, visual bearings were taken on the lightship. The derived data are adduced in table 6 (all of the hydrochemical analyses were made by L.S. Ponomarenko).

As will be seen from table 6, the salinity and phosphates content increased with depth. On the other hand, the temperature, oxygenation, nitrites content and the pH diminished. It it very significant that all the indices of the hydrological and hydrochemical regime remained almost unchanged throughout the 24-hour period at each horizon. Meanwhile, on 70
October 30, 1954, diurnal vertical migrations and the resulting fluctuations in the trawl catches were quite clearly manifested in the north-central region.

All the above-adduced data proved that the diurnal vertical migrations of the aquatic animals are accomplished in spite of rather than because of the effect of the hydrological and hydrochemical regime. For the temperature and chemism of the water at the middle horizons are normally different than in the near-bottom region. It would appear that these differences in the aquatic regime may create an almost impassable barrier for the marine animals. In point of fact this is not so: twice in 24-hours the migrating organisms rapidly and freely change physico-chemical environments.

Table 5

Temperature and chemical composition of the water at various horizons on April 15, 1953

Время взятия пробы в часах и минутах 1.	Горизонт в м 2.	Температура в °С 3.	Соленость в ‰ 4.	Плотность 5.	Насыщение кислородом в % 6.	Фосфаты в мг/м³ 7.	Активная реакция 8.
0—00	0	1,14	34,74	0,902785	99	24	8,01
	50	1,12	34,76	0,902787	99	24	8,01
	145	1,14	34,74	0,902785	98	24	8,01
3—55	0	1,06	34,67	0,902780	99	23	8,01
	50	0,98	34,65	0,902779	99	23	8,01
	145	1,03	34,65	0,902779	98	23	8,01
8—05	0	1,08	34,72	0,902784	99	23	8,01
	50	1,00	34,72	0,902784	100	23	8,01
	151	1,02	34,74	0,902786	96	23	8,01
13—00	0	1,55	34,70	0,902779	100	23	8,04
	50	1,18	34,70	0,902782	99	23	8,04
	129	1,43	34,72	0,902781	97	23	8,04
17—25	0	1,21	34,67	0,902779	100	23	8,02
	50	1,01	34,67	0,902780	100	23	8,02
	145	1,11	34,78	0,902789	98	24	8,02
23—45	0	1,25	34,67	0,902779	99	23	8,01
	50	1,05	34,67	0,902780	99	23	8,01
	141	1,25	34,76	0,902786	—	—	—

Key: 1 - Time of taking sample, in hrs and mins.
2 - Horizon, in m
3 - Temperature, in °C
4 - Salinity, ‰
5 - Density
6 - Oxygenation, %
7 - Phosphates, mg/m^3
8 - pH

Turning to table 6 we notice that at night, at a depth of 100 m the temperature equalled almost 5°C, while in the daytime it scarcely exceeded 3° near the bottom. As indicated by the echo sounder, the fish had migrated from the bottom to the middle layers and back again in the course of the 24-hour period, experiencing while it did so a temperature change of almost 2°.

The findings of N.N. Zubov [27], indicate that in the south-western part of the Barents Sea, at depths of 25-50 m the diurnal temperature fluctuations are as great as 2.57°, which is due to the ebb and flow of the tides. Since the periodicity of the tides does not coincide with the alternation of light and darkness, a migrating fish is frequently subjected to very large changes in the temperature (and chemism) of the water. 71

Table 6

Temperature and chemical composition of the water at various horizons

1. Дата	2. Время взятия пробы	3. Горизонт в м	4. Температура в °	5. Соленость в ‰	6. Насыщение кислородом в %	7. Фосфаты в мг/м³	8. Нитриты в мг/м³	9. Активная реакция
10.								
29 октября	19—20	0	5,5	34,85	95	23	1,35	8,01
		25	5,38	34,85	95	23	1,50	8,02
		50	5,37	34,85	94	23	1,50	8,02
		100	4,98	34,94	91	25	11. Следы	7,98
		270	2,36	35,01	89	27	0	7,97
30 .	1—35	0	5,5	34,63	96	20	1,50	8,03
		25	5,41	34,63	96	20	1,50	8,04
		50	5,40	34,67	95	20	1,50	8,02
		100	4,92	34,85	91	21	11. Следы	7,98
		235	3,67	35,01	90	31	0	7,97
30 .	8—45	0	5,5	34,60	95	23	1,50	8,03
		25	5,36	34,67	96	23	1,50	8,02
		50	5,38	34,67	96	23	1,42	8,02
		100	4,90	34,88	92	24	Следы	7,97
		233	3,56	35,01	90	25	0	7,97
30 .	16—00	0	5,4	34,60	96	23	1,50	8,02
		25	5,40	34,61	96	23	1,35	8,01
		50	5,52	34,88	95	24	0,90	8,01
		100	4,88	34,91	94	26	0	7,98
		235	3,06	35,01	93	28	0	7,97
30 .	20—45	0	5,3	34,58	96	22	1,50	8,03
		25	5,22	34,60	96	22	1,35	8,04
		50	5,11	34,87	92	24	0,90	8,02
		100	4,76	34,94	92	26	Следы	7,99
		253	2,14	35,05	91	28	0	7,97

Key: 1 - Date
2 - Time of taking sample
3 - Horizon, m
4 - Temperature, °C
5 - Salinity, ‰
6 - Oxygenation, %
7 - Phosphates, mg/m³
8 - Nitrites, mg/m³
9 - pH
10 - October
11 - Traces

The planktonic animals also withstood drastic temperature fluctuations in the course of the diurnal vertical migrations. Thus, Calanus finmarchicus ascends in summer from layers with a temperature of 8.5° to layers with a temperature of 22-24° [51]. The Black Sea organism Sagitta euxina ascends at night from deep layers with a temperature of less than 10° to surface layers with a temperature of 19-23° [53].

In summer, the planktonic crustacea of the Polar Seas remain at a constant depth, thereby experiencing drastic fluctuations in the physico-chemical properties of the water [10,11]. In particular, the temperature may change by as much as 3° in the course of the 24-hour period.

The temperature differences between the surface and the ocean deeps are especially large in the tropical seas. In the Atlantic, at the 35th parallel, the surface temperature is 7° higher than the temperature at a depth of about 600 m. At the 20th parallel the difference in the temperature of the water at the indicated horizons was as great as 16° [101]. Meanwhile, vertical migrations of fishes also occur in equatorial latitudes. Nichols and Murphy [103] very colourfully describe the massing of 72
deep-water organisms near the surface of the sea (this was observed on a March night at the 4th degree of lattitude, off the coast of Columbia). Typically deep-water fishes are also to be seen at the surface, for example, Myctophum aurolaternatum. Having ascended from the deeps, the specimens were naturally subjected to a very substantial change in the temperature of the water.

It is important to note that migrating aquatic animals move between horizons with differing temperatures very rapidly. M.M. Knipovich [33] has reported on the Caspian mysids as having ascended 90 m in the space of

an hour and a quarter. In certain of the Atlantic crustaceans, the speed of vertical migration is as great as 125 m/hr [113]. The South Atlantic Euphausia frigida, according to Hardy and Gunther [89], migrates over a distance of almost 200 m along the vertical, in the space of 1-2 hours. Calanus simullimus makes an ascent of 50 m in an hour. M.E. Vinogradov [19] reports that the Pacific Metridia okhotensis descends at an average speed of more than 80 cm/min, while the rate of descent of other, larger plankters even reaches several meters per minute. V.G. Bogorov indicates that, for the Caspian copepod Eurytemora grimmi, the rate of ascent and descent is identical, being 2 cm/sec.

Thus, when accomplishing diurnal vertical migrations, the animals easily surmount steep temperature gradients.

Citing as an example the Baikalian fauna, A.A. Zakhvatkin [22] shows that animals accomplishing diurnal vertical migrations are highly eurythermal. The temperature neither causes nor regulates the vertical migrations, although it may sometimes restrict them. Thus, M.E. Vinogradov [19] notes that, in the Sea of Okhotsk and the Bering Sea, diurnal vertical migrations of the zooplankton are of relatively small extent. This is due to the very cold intermediate layer of water, which serves to obstruct the route taken by the migrants into the deep region. The same is reported by K.A. Brodskii [14] with respect to the plankton of the northwestern part of the Sea of Japan. Yu.Yu. Marti [45] indicates that in the region of Gusinaya Bank it is as if the steep vertical temperature gradient is holding the fish close to the bottom and thereby promoting an increase in its demersal concentrations. According to V.M. Nikitin [52], the vertical distribution of the Black Sea zooplankton throughout the year is delimited by definite

isotherms. A.P. Kusmorskaya [43] and M.M. Kamshilov [29] mention that downward penetration of the planktonic crustacea ceases at a layer with a definite minimal temperature.

A sudden invasion of cold water masses may not only disrupt the course of the diurnal vertical migrations, but even lead to mass deaths of fishes and other aquatic animals [47, 81, 88, 94, 97, 110]. In all such cases, a change in the temperature stands out as a hindrance to diurnal vertical migrations rather than the driving force.

Roughly the same can be said about the chemism of the water. S.V. Bruevich [16] notes that in the Barents Sea the content of phosphates, nitrites and silicic acid changes non-periodically or with a period exceeding the diurnal (under the influence of the tides). Consequently, fluctuations in the chemism of the water are not synchronized with the vertical migrations of the aquatic animals..

Baikalian pelagic forms, migrating in the mid-water, experience very wide fluctuations in physico-chemical factors, especially in July, when the stratification of these factors is most marked [22]. Planktonic animals of the South Atlantic, in migrating, move between horizons that are noticeably different with respect to pH and oxygen content [89].

V.G. Bogorov [6] notes that the vertical distribution of the Barents Sea and White Sea plankton bears no relation to the oxygen content. Of course, the migrating animals do not penetrate to layers where 73
the oxygen content is below a certain minimum, for example, into the deep regions of the Black Sea [55]. In other words, the oxygen, like the temperature of the water, is capable of delimiting but not directing the

diurnal vertical migrations of aquatic animals.

The migrants are also subjected to a rapid and substantial change in the pressure of the water. Echo sounder recordings indicate that in the course of several hours, cod and haddock accomplish a 100 m ascent from the bottom. This entails a drop in the pressure of approximately 10 atm. Even larger migrations of fishes along the vertical have been reported. N.M. Knipovich [33], citing the data of Jort, makes mention of North Atlantic fishes accomplishing nocturnal ascents from depths of 1500 m to depths of 150 m. Consequently, these fishes are subjected to a change in the pressure of more than 100 atmospheres.

The amplitude of the vertical migrations of invertebrate animals is also very great. Waterman, Nunnemacher, Chase and Clark [113], after collating a vast body of published data, pointed out that of all the planktonic animals of the Antarctic waters, the greatest diurnal migration is accomplished by Pleuromamma robusta. This copepod ascends to the upper 100-meter layer of water at night, and descends by day to depths of more than 600 m. As noted by M.E. Vinogradov [18], diurnal vertical migrations of the zooplankton in the Pacific Ocean have been traced to a depth of 750 m.

Consequently, even enormous changes in the water pressure do not serve as a hindrance to animals accomplishing diurnal vertical migrations.

THE BIOLOGICAL SIGNIFICANCE OF DIURNAL VERTICAL MIGRATIONS OF AQUATIC ANIMALS

As was indicated in the preceding sections, of all the hydrometeorlogical factors it is only the illumination of the sea which stands out as the driving force behind the diurnal vertical migrations of fishes and the zooplankton. The remaining physical chemical properties of the aqueous environment can have only an indirect effect on migration. Thus, the depth to which light penetrates is dependent on the transparency of the water. Accordingly, in turbid water vertical migrations have a smaller amplitude, as is seen in the case of fishes belonging to the Clupeidae [57,106]. The penetration of light into the mid-water may be hampered by an ice sheet. It is for this reason that in Baikal, diurnal vertical migrations of the zooplankton are much less pronounced in winter than in summer [36,37].

As was pointed out earlier, a layer of desalinated or very cold waters may limit the scope of diurnal vertical migrations [14,19,52]. Finally, as asgerted by A.A. Zakhvatkin [22] and M. M. Kozhov [37], the effect of the wind is manifested chiefly as a disturbance of the true course of the diurnal vertical migrations.

What is the explanation for the exclusive role of light in regulating the diurnal vertical migrations of aquatic animals? What is it specifically that is vitally important to the migrants: the light itself or certain conditions, linked with a definite degree of illumination?

Many investigators are inclined to regard exposure to light as a physiological factor, necessary for the normal vital activity of aquatic

animals, and therefore even determining the horizon of their habitation. Thus, in the opinion of V.G. Bogorov, the zooplankton surmount very drastic changes in the physico chemical conditions, in striving to maintain a horizon of habitation that is optimal with respect to conditions of illumination [11]. A highly staunch advocate of a similar point of view is M.E. Vinogradov [19], according to whose opinion planktonic animals accomplish very deep migrations, in escaping from the "injurious effect of light". The role of the red pigment in Calanus supposedly consists of protecting the crustacean against light during long periods of proximity to the surface. L.A. Zenkevich [26] also considers that vertical 74
migrations of plankton are associated with negative phototropism. It is possible that protection against natural enemies plays some kind of role in the shaping of this phenomenon, although hardly a dominant role. According to Zenkevich, the avoidance of light is due to the directly injurious effect it has on aquatic animals.

Nevertheless, there is as yet no convincing evidence of the injuriousness of light in the case of planktonic animals. On the contrary, according to the experimental findings of Lebour [95], exposure to light does not even affect the pigmentation of developing euphausiids. It is difficult to accept that the suggested "injurious effect" would also be characteristic of moonlight, which, as is well known, causes vertical migrations of fishes [107], and plankton [19,35]. Finally, vertical migrations are even caused by light which has penetrated through a thick sheet of ice [36,37].

The hypothesis with respect to the independent importance of light as a factor in vertical migrations hampers the solving of the

following problems. Why do vertical migrations occur non-uniformly, depending on the sex and stage of development of the individual [5,12,13,29, 102]? Why do not all individuals participate in migrations, even those that are identical as to sex and stage of development [89,98]? Why is a deep descent sometimes begun earlier than the first signs of daybreak [19, 22,98]?

Another explanation for the phenomenon we have been discussing appears to be much more satisfactory. There exist numerous data with respect to the close relationship between diurnal vertical migrations of plankton and the fishes devouring it. In the case of herring this has been pointed out by Lebour [95], Lucas [96] and Bogorov [7]. Small hakes have also been reported to ascend to the upper layers in pursuit of the euphausiidae on which they feed [90]. Cod and haddock regularly forsake the demersal horizons in pursuit of plankton and pelagic fishes [23,24, 46,76,77]. Citing also his own observations and the age-old experience of fishermen, M.M. Kozhov [35] points out that the whitefish repeats the vertical migrations of planktonic crustaceans. N.I. Chokhuri [68] considers that diurnal vertical migrations of the zooplankton can be regarded as one of the most important factors causing diurnal vertical migrations of anchovies. E.V. Borutskii [13] also notes that, simultaneously with diurnal horizontal and vertical migrations of crustaceans, corresponding migrations of fishes are seen. The close connection between diurnal vertical migrations of fishes and zooplankton is also cited by N.I.Chugunova and K.I. Yudanov [69], and N.I. Kashkin [30].

Carnivorous representatives of the zooplankton, like fish, pursue their prey during diurnal vertical migrations. M.E. Vinogradov [17]

mentions the role of such migrations in the feeding of deep-water plankton. L.A. Ponomareva [60,61] considers that the euphausiids feed on copepods primarily in the upper 50-meter layer of the water, that this reaches maximum intensity at night and in the evening. Lebour also makes mention of the euphausiids feeding mainly in the upper horizons [95].

As regards the herbivorous planktonic forms, their ascent to the surface is due to the abundance of phytoplankton in the upper layers of the water. N.V. Morozova-Vodyanitskaya [50] reports that, in the Black Sea the quantity of phytoplankton sharply decreases at night on account of its being consumed by the zooplankton. Gauld [87] showed that Calanus finmarchicus, in accomplishing diurnal vertical migrations, feeds principally in the surface horizons.

As mentioned by K.A. Brodskii [14], V.L. Khmyznikova [67], V.N. Nikitin [54], M.E. Vinogradov [18], A.E. Kriss, V.I. Biryuzova, E.A. Rukina [41], and A. Trofimov [65], the biomass of the plankton is normally at a maximum in the upper horizons, decreasing with depth. It is only in a small number of water bodies that the biomass of individual 75
groups increases with depth. An example of this would be the distribution of microorganisms in the Black Sea [40].

Thus, in ascending to the upper layers, the herbivorous representatives of the zooplankton enter a zone which is rich in food. Why, however, do they not remain there throughout the 24-hour period?

Many facts and theories indicate that, for the zooplankton, the daytime descent to deep regions is of protective value. In actual fact, plankton-eating fishes seek out their prey, being guided mainly by visual perceptions. Consequently, the zooplankton near the surface are

relatively safe only during the night. A daytime migration deep into the mid-water is not a passive submergence. As was shown by V.G. Bogorov [8], when accomplishing vertical migrations, the Caspian Eurytemora grimmi moves at almost the same speed when ascending and descending, attaining this speed by active swimming motions. N.M. Knipovich [34] makes mention of the extremely rapid submergence of the Black Sea Calanus. According to Dietz [83], in the evening the Pacific zooplankton ascend at a rate of 15-18 feet in one minute, the corresponding rate of descent in the morning being 10-15 feet.

Thus, it is not because of the "destructive effect" of light that the planktonic animals accomplish deep migrations, but rather on account of the safety and nourishment to be had under conditions of poor illumination. This point of view is defended by many authors, the most persuasive of whom are M.M. Kozhov [35] and I.I. Nikolaev [56]. We come to understand why not all of the individuals take part in diurnal vertical migrations. Those whose alimentary tracts are particularly well-filled remain on the bottom not only in the daytime, but also at night, without taking part in the next ascent to the surface [89]. The differing requirement for food is also explained by the non-uniform vertical distribution of the males and females, both young and old individuals. Some planktonic forms begin their descent even before daybreak. This makes it possible for them to reach a safe horizon early.

Consequently, the biological import of vertical migrations for zooplankton can be formulated as follows: the securing of food in the most safe situation. Diurnal vertical migrations of fishes are also, in the main, feeding (trophic) in character. M.I. Kuznetsov, who is the most senior captain-scout of the Murmansk trawling fleet, was undoubtedly right

when he pointed out that it is necessary to allow for the vertical migration of a fish, since it is to the place where the food is manifested that the fish goes [42].

We can hardly assume that light has a "destructive effect" on the fish. As indicated by our observations from a diving bell [44], small cod and haddock remain on the bottom in shallow bays when the light is at a very high intensity, without showing any symptoms of stunting.

At first glance, the reasons leading to diurnal vertical migrations of a cod when it is feeding on the capelin (in the spring) and herring (in autumn) are not completely clear. In spring, a capelin preparing to spawn hardly feeds at all and does not leave the surface layer of the water. Similarly, a herring will remain in the surface layer in the autumn. Why is it that, during these seasons, a cod feeding on capelin or herring, will accomplish true vertical migrations and ascend to the surface only at night, rather than at any time during the 24-hour cycle?

In order to reply to this question it is necessary to keep in mind that capelin and herring, like the majority of the plankton-eating fishes, orientate themselves in the environment chiefly by means of vision. In the bodies of these fishes there are no or almost no lateral line organs, and in the brain the olfactory lobes are relatively weakly developed [59]. In cod fishes, visual perceptions play a much smaller role. The eyes of the cod and haddock are relatively small, the lateral line organs are well-developed on the head and trunk, and the chin barbel performs a tactile function. In the brain, both the visual and olfactory organs are well-developed.

Experiments performed on certain representatives of the Gadidae, 76
for example on the hake [1,2], show that in the seeking out of food the specimens that were tested are guided more by touch than by vision. Although such experiments have not yet been conducted with cod and haddock, many data attest to the very important role of olfactory and tactile perceptions in the behaviour of these fishes. It is only through the participation of olfaction that we can explain, for example, the greed with which the cod grasps a purified piece of mollusc meat [76], the propensity of cod to get into long-lines at night, and a number of other facts.

A record exists of the catching of a blind specimen of a cod, which had subsisted and spawned normally [38].

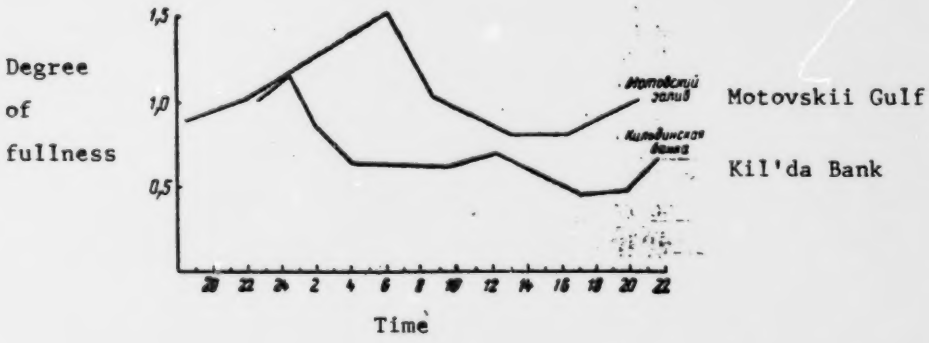

Fig. 6. Degree of fullness of the stomachs of cod at different times of the day and night

It is quite clear that cod and haddock can hunt for pelagic fishes more successfully in darkness than when it is light, and therefore that it is precisely at night that they ascend to the surface. An analysis of the stomach contents of a cod shows that in the spring and autumn it feeds more intensively during the night than by day. Illustrated in figure

6 is the fullness of the stomachs of cod at various times of the day and night. The material was collected during the opening days of May, 1953. The stomachs contained almost exclusively capelin. It was readily apparent that the fullness of the stomachs increases at night and decreases during the day.

A similar picture was observed in the autumn of 1954, when herring played an important role in the feeding of cod. As will be seen from figure 7, both the overall index of fullness and the index of fullness for herring is higher at night than during the day.

According to the findings of E.S. Zadul'skaya and K.S. Smirnov [21], the fullness of a cod's stomach is normally maximal during the hours of 0400-0800, that is, after intensive nocturnal feeding.

Given that the main food of the cod or haddock are bottom-dwelling organisms, the fullness of the stomachs will be higher during the daytime, when the feeding fish is situated near the bottom. Presented in figure 8 are the indices of fullness of the stomachs of haddock, caught at different times of the day and night on Kanin Bank (feeding analyses performed by R. Tseeb, a co-worker of the Murmansk Biological Station). From each trawl, 25 specimens of haddock were taken for the analysis of the stomach contents. It is noteworthy that in the stomachs of the haddock caught at night, herring was often detected.

A somewhat special case was noted in April of 1954. The inshore areas were visited by exceptionally large concentrations of capelin, which remained in the entire column of water from the surface to the bottom. During this period, no vertical migrations of cod and haddock were observed, which is quite understandable, since these fishes find their food in

abundance at any horizon, in particular near the bottom. In the case being described, the absence of a diurnal vertical migration is fully understandable when their trophic character is accepted, but cannot be 77
explained according to the "avoidance of lights" hypothesis. For in April there is a clearly defined alternation of the light and dark period of the day.

Nocturnal ascents to the surface with intensification of feeding are not only typical of cod and haddock, but also of a number of other fishes, for example the fry of kilka and percarina. This was pointed out by N.I. Kashkin [30], who correctly links the diurnal vertical migrations of the fishes that he studied with feeding, but is unable to explain why percarina feeds more intensively at night, and kilka - by day. Nevertheless, the reason is very simple: in the pursuit of prey, the kilka is guided primarily by vision, and the percarina - by other receptors. It is therefore biologically advantageous for the percarina to hunt in darkness, for which purpose it ascends to the surface at night. It is not the light itself that is important to the migrants, but rather the conditions resulting from the illumination which pertain to the pursuit of prey or the avoidance of predators.

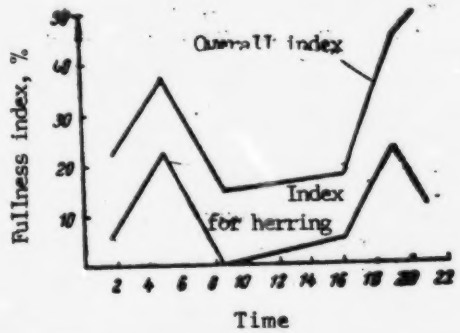

Figure 7. Index of fullness of the stomachs of cod at different times of the day and night

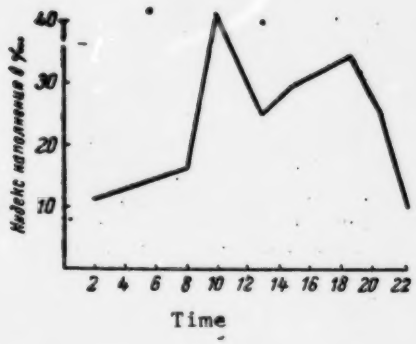

Figure 8. Index of fullness with bottom fauna of the stomachs of haddock, at different times of the day and night

We therefore consider that, for animals accomplishing diurnal vertical migrations, light plays the role of an orientating factor. Movement towards a zone where there is a specific light intensity is a reflex action, as has been correctly pointed out by S.G. Zusser [28], although he erroneously regards them as conditioned reflexes. It is, of course, impossible to speak of the conditioned (acquired) reflexes of just-hatched herring larvae. According to some data [82], even the eggs of plaice react to light, in sinking into the middle layers by day and rising to the surface at night. Thus, it is more correct to regard the movements of aquatic animals that are caused by light as conditioned (innate) reflexes. A reflex to light, however, can be suppressed by a reflex to the presence of food. A fish will not leave horizons abundantly rich in food, regardless of any fluctuations in the illumination.

THE STUDY AND USE OF DIURNAL VERTICAL MIGRATIONS OF COD AND HADDOCK

As was mentioned at the outset, diurnal vertical migrations of cod and haddock noticeably influence the progress of trawling. Captains of fishing trawlers are obliged to keep count of regular fluctuations in catches throughout the 24-hour period. In order to make optimum use of

the fishing situation, all of the preparatory operations (for example, the rigging, replacement and repair of the trawls) should be relegated to the nighttime hours. It is also desirable that transfers between squares be accomplished at night. The maximum number of trawlings must be made in the day, during the hours of the best catches.

In a discussion of diurnal vertical migrations, the workers of 78
the /scouting fleet must not be overlooked. When exploring an area, the time of day must be taken into consideration in evaluating the trawling results. Small takes, obtained at night, are not necessarily indicative of an absence of fish: a check on the same region during the day may yield vastly better results.

In all cases, when fishermen or /scouts are encountering diurnal vertical migrations of cod and haddock, hydroacoustic techniques have an enormous role to play. As indicated by the experience of recent years, recording echo sounders detect fish concentrations in the mid-water with great accuracy and reliability. Accordingly, for the correct assessment of the capabilities of the industry it is necessary to keep a close watch on the readings of the echo sounder, which must be in a fully serviceable condition at all times.

Today, diurnal vertical migrations of cod and haddock can be utilised when catching the latter by midwater trawl, which can give us a more precise understanding of the biological patterns of fish migrations.

CONCLUSIONS

1. In spring and autumn, when there is a regular alternation of the dark and light period of the day, cod and haddock accomplish diurnal vertical migrations, ascending into the mid-water at night, and descending by day into the /near-bottom horizons.

2. Diurnal vertical migrations substantially affect the progress of trawl fishing, as cod and haddock which have ascended into the middle layers cannot be caught by bottom trawl. Daytime catches may exceed nighttime by more than 40%.

3. Of the hydrometeorological factors, fluctuations in the illumination exert a regulating influence on diurnal vertical migrations of cod and haddock. Neither the temperature nor the chemism of the water direct the diurnal vertical migrations: they may only limit or interfere with them.

4. In accomplishing regular migrations in the mid-water, cod and haddock enter poorly illuminated horizons that are rich in food, which enables them to pursue their prey most efficiently.

5. A nocturnal ascent to the surface provides food for the zooplankton. A deep descent during the daytime saves the zooplankton from being eaten by the fishes.

6. In diurnal vertical migrations of aquatic animals, light itself is not the vitally important factor: it merely orientates the migrants to move to the conditions which are most suitable for feeding and avoidance of enemies.

7. When organizing the work of fishing trawlers, the effect of diurnal vertical migrations on catches of cod and haddock must be taken into consideration. Secondary and preparatory operations should be relegated to the night hours. During the daytime, every effort must be made to complete the maximum number of trawlings. Fish concentrations in the mid-water must be regularly monitored by means of an echo sounder.

8. The development of the mid-water trawl will enable the industry to make more active use of diurnal vertical migrations of cod and haddock, thereby greatly expanding its capabilities.

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